

Fruit Flies

(Tephritidae):

Phylogeny
and Evolution
of Behavior

Edited by

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Cover Photographs: (Top to Bottom) (1) Regurgitated droplets deposited by *Anastrepha serpentina* female. These droplets are then reingested by the same female. (Photograph by R. Wilson.) (2) Mating pair of *Anastrepha serpentina*. (Photograph by R. Wilson.) (3) Feeding in damaged guava by females of *Anastrepha ludens* (head in hole) and *A. fraterculus* (entire fly in hole). (Photograph by E. Piedra.) (4) Male of *Ceratitis capitata* releasing pheromone during calling bout. (Photograph by K. Kaneshiro.)

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15 Behavior of Flies in the Genus *Anastrepha* (Trypetinae: Toxotrypanini)

Martín Aluja, Jaime Piñero, Isabel Jácome, Francisco Díaz-Fleischer, and John Sivinski

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15.1 INTRODUCTION

Flies in the genus *Anastrepha* Schiner offer a unique opportunity to study behavior using a comparative approach. The species that have been studied to date have revealed a remarkably plastic, variable, and complex behavioral repertoire. Male calling rhythms and behaviors performed during sexual encounters are good examples of this. Some species, like *A. robusta* Greene, perform elaborate in-flight loops during calling (wing fanning) bouts while other species, like *A. aphelocentema* Stone, *A. cordata* Aldrich, or the closely related species *Toxotrypana curvicauda* Gers-taecker, stand still and do not wing fan during the entire daily calling period (calling in these three species is discernible because males puff pleural glands and release a sexual pheromone). With respect to calling rhythms, some species call at dawn (*A. cordata*) while others do so at sunset (e.g., *A. spatulata* Stone). Another *Anastrepha* behavior where great variability is observed is oviposition. For example, species like *A. obliqua* (Macquart) lay strictly one egg/clutch, while others, like *A. grandis* (Macquart), are able to lay more than 100 eggs/clutch. Furthermore, there are a few species like *A. hamata* (Loew) that never mark a fruit, while many others deposit a host-marking pheromone after an oviposition bout, for example, *A. spatulata*, *A. leptozona* Hendel, *A. alveata* Stone, *A. ludens* (Loew), *A. grandis*, *A. fraterculus* (Wiedemann). This great variability in the behavioral repertoire, added to the fact that we now have a fairly well-supported phylogeny for the 197 known species (Norrhöm et al., Chapter 12; and McPheron et al., Chapter 13), opens up the opportunity to build a behavioral phylogeny of unprecedented scope.

In this chapter, we will first provide a historical review of studies on *Anastrepha* behavior and summarize relevant information on their biology and natural history. Then, we will describe the few known facts about larval behavior, review known adult diel rhythms of activity, and address in detail each of the most important behaviors exhibited by *Anastrepha* adults: trivial movements, feeding, oviposition, mating, and shelter seeking and resting. In doing so, we will review all previously published work along with unpublished information recently generated on rare species such as *A. acris* Stone, *A. alveata*, *A. aphelocentema*, *A. bahiensis* Lima, *A. bezzii* Lima, *A. cordata*, *A. distincta* Greene, *A. leptozona*, *A. hamata*, and *A. spatulata*. Whenever possible, we will compare behavioral data on *Anastrepha* with relevant information on *T. curvicauda*. This species belongs to the genus that may be the sister group of *Anastrepha* or may even fall within *Anastrepha* (formal analysis of phylogenetic relationships of *Anastrepha* and *Toxotrypana* can be found in Norrhöm et al., Chapter 12, and McPheron et al., Chapter 13). Our intent is also to lay down relevant facts for the formal discussion of the evolution of fruit fly behavior in the last part of this book (Drew and Yuval, Chapter 27; Díaz-Fleischer et al., Chapter 30; and Sivinski et al., Chapter 28).

15.2 HISTORY OF STUDIES ON ANASTREPHA BEHAVIOR

When reviewing the history of studies on *Anastrepha* behavior, several highlights emerge: (1) there is a series of highly insightful, but for the most part anecdotal, observations made by Mexican and American naturalists at the beginning of the 20th century in Mexico and Puerto Rico (L. de la Barrera and A. Rangel cited by Herrera 1905; Crawford 1918; 1927; Picado 1920; McPhail and Bliss 1933; McAlister et al. 1941; also see review by Baker et al. 1944). In our opinion, all of these authors deserve credit as pioneers in the study of the biology and behavior of *Anastrepha*. Between this period (1900 to 1944) and the burst of activity in the late 1970s to early 1980s, work on *Anastrepha* behavior was virtually halted. (2) Most in-depth studies on *Anastrepha* behavior are restricted to seven economically important species: *fraterculus*, *grandis*, *ludens*, *obliqua*, *serpentina* (Wiedemann), *striata* Schiner and *suspensa* (Loew) (e.g., Nation 1972; Perdomo 1974; Dodson 1982; Dickens et al. 1982; Aluja et al. 1983; Burk 1983; Malavasi et al. 1983; Morgante et al. 1983; Robacker and Hart 1985; Hendrichs 1986; Sivinski and Webb 1986; Sivinski 1988; 1989; Aluja

et al. 1989; Robacker et al. 1991; Silva 1991; Silva and Malavasi 1993; Aluja and Birke 1993; Aluja et al. 1993; Sivinski et al. 1994). (3) Most studies on *Anastrepha* behavior stem mainly from three countries: Brazil, Mexico, and the United States (also one study from Costa Rica, Hedström 1991; in addition to references under item 2 above, Silva et al. 1985; Polloni and Silva 1987; Selivon 1991; Morgante et al. 1993; Aluja 1993a).

The first anecdotal observations made on aspects of behavior of an *Anastrepha* species are arguably those on *A. ludens*, described in 1873 by the German taxonomist H. Loew as *Trypeta ludens* and in early works often called the "orange worm." Alfonso Herrera (1900) compiled some observations by a series of U.S. naturalists working in Mexico between 1881 and 1897, indicating that *A. ludens* females deposited their eggs in the skin of oranges and that larvae exited the fruit and buried themselves in the ground to pupate. At a later date, Herrera (1905) cited a series of observations by Leopoldo de la Barrera and Amado Rangel (Mexican Ministry of Agriculture agents) on the "intelligence" of *A. ludens* adults and larvae. In the original text by Herrera (1905), Rangel and de la Barrera describe how larvae extracted from the pulp, "crawl day and night experiencing sensations of fear and malaise. If touched they contract and cease moving." Once development is completed "they frantically search for a dark site to pupate." While still feeding in the fruit "some larvae peep out through a hole drilled by them to breathe." On occasion, if the ripe fruit does not drop from the tree, some larvae "that cannot wait any longer" jump out of it from considerable heights. With respect to the adult fly, it is mentioned that "their senses are more perfect and their intellectual manifestations more complex." These senses "are mainly determined by sensations of fear, hunger and desire, especially a maternal desire that forces females to lay their eggs in a protected spot underneath the skin of an orange." These authors noted that females did not lay eggs in many parts of the orange, but instead they preferred one single site, perhaps "to economize time and labor." Rangel and de la Barrera were intrigued by the fact that females did not lay more than six to ten eggs per fruit and only in one slice of an orange. They attributed this to the "intelligence" of the female which "understood that if they deposited all the germs carried in their ovaries in one single fruit, there would not be enough food for all the progeny." In other words, "the *Trypeta* mother has sufficient insight to avoid putting on board all her progeny in one boat but instead distributes it in 8, 10 or more fruits." Rangel and de la Barrera also noted that guavas, a fruit smaller than oranges, hosted fewer larvae and that flies would only lay one egg in cherries because of the small size of this fruit.

When describing the general behavior of adults, Rangel and de la Barrera mentioned that the movements of flies are "very fast." If exposed to direct sunlight "flies move nervously." When on a leaf flies "exhibit excessive limidness, frequently turning graciously 360 degrees to face their enemy." Adults "like" to feed on juices oozing from fruit, especially oranges and guavas. In orchards, flies "like" to rest on the underside of leaves. Females prefer to sting mangoes in the "middle section" of the fruit. Oranges are always stung in the bottom part of the fruit. When a female is ready to oviposit, "it moves on the surface of the fruit in slow motion while searching for an appropriate spot. As soon as an ideal location is found it turns rapidly, inserts its ovipositor perpendicularly and stays motionless for up to two minutes. This procedure can be repeated 3 or 4 times before moving on to another fruit." Rangel and de la Barrera indicated, further, that females "prefer" to attack fruit that is in well-shaded parts of a tree and "avoid" fruit in branches that stick out from the crown (sun exposed). Fruits with a thick albedo are always "preferred" over those with a thin albedo.

All these insightful observations refer to phenomena such as clutch size regulation, oviposition site selection, enhanced fitness through efficient resource use, and physiological state (sensations of "fear," "hunger," "desire," "malaise"). We wanted to cite them specifically because few people know or have access to them. Other pioneering work on *Anastrepha* behavior is reviewed by Díaz-Fleischer and Aluja (Chapter 3).

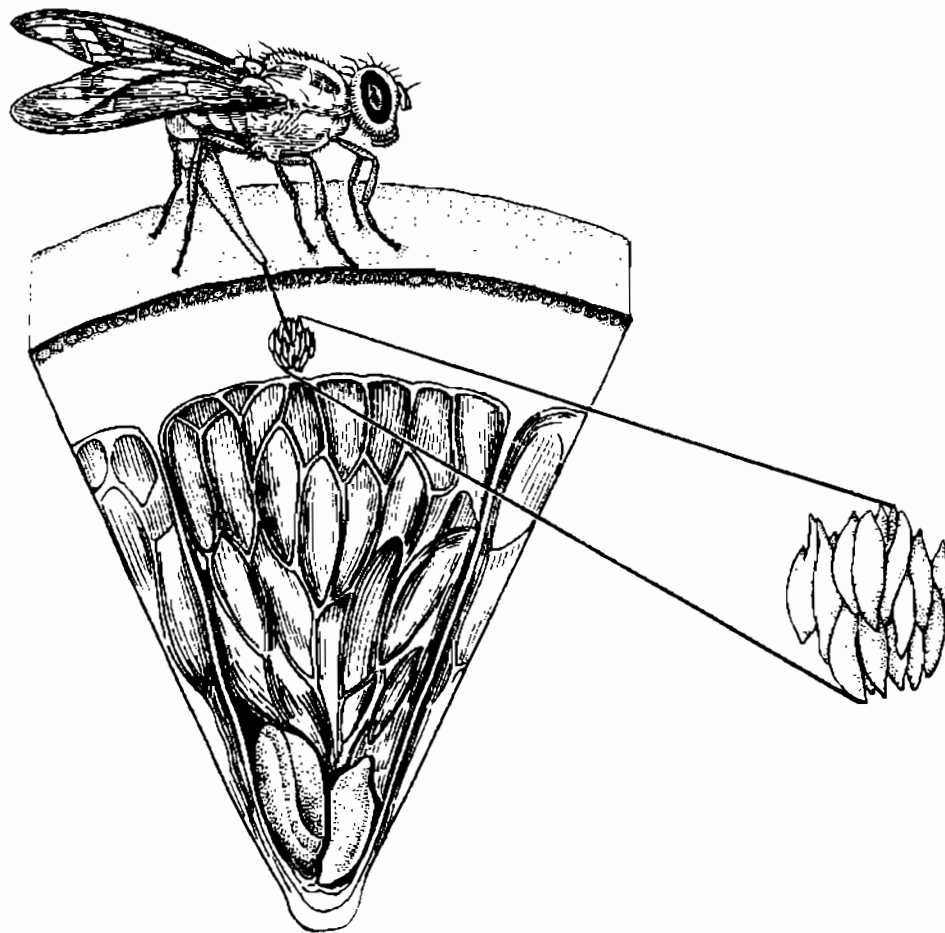


FIGURE 15.1 *Anastrepha ludens* female depositing a clutch of eggs in the albedo of a grapefruit. (Courtesy of Andrea Birke.)

15.3 ASPECTS OF *ANASTREPHA* BIOLOGY AND NATURAL HISTORY RELEVANT TO BEHAVIOR

Anastrepha is endemic to the New World and is restricted to tropical and subtropical environments (Aluja 1994). Its range covers part of North America (states of Florida and Texas in the United States and all of Mexico), Central and South America (except Chile) and most of the Caribbean Islands (Hernández-Ortiz and Aluja 1993). The basic life cycle is similar among all *Anastrepha* species (see detailed review by Aluja 1994): females deposit their eggs in the epi- or mesocarp region of host fruit or, in some species such as *A. hamata*, in developing seeds (Color Figure 14*). Eggs are laid singly (e.g., *A. obliqua*) or in clutches (e.g., *A. ludens*) (Figure 15.1). The larvae of many species feed on the fruit pulp but it appears that the larvae of the primitive species (see Norrbom et al., Chapter 12, and McPherson et al., Chapter 13) feed on seeds (e.g., *A. cordata*, *A. hamata*, *A. bezzii*, *A. sagittata* (Stone), *A. pallens* Coquillett and *A. spatulata*; McPhail and Berry 1936; Baker et al. 1944; Santos et al. 1993; Hernández-Ortiz and Pérez-Alonso 1993; M. Aluja and M. López, unpublished data). Larvae of the close *Anastrepha* relative, *T. curvicauda*, also feed on

* Color Figures follow p. 204.

seeds (Peña et al. 1986). However, caution is warranted in drawing generalizations from this. *Anastrepha ludens*, for example, is well known for the damage it inflicts on commercial citrus groves. When attacking fruits in the genera *Citrus* or *Mangifera* (both introduced to the American Continent), larvae always feed on the albedo or the fruit pulp, but never on seeds. In contrast to this, in fruits of what are believed to be their ancestral host plants (*Sargentia greggii* S. Wats. and *Casimiroa edulis* Llave and Lex.), they basically feed on the seeds alone (*S. greggii*) or on both seeds and pulp (*C. edulis*) (Plummer et al. 1941; F. Díaz-Fleischer, unpublished data). Thus, widespread pulp feeding in *A. ludens* larvae could be a derived behavior that appeared recently as the result of the introduction of hosts such as *Citrus sinensis* L. (Osbeck) and *M. indica* L.

An interesting aspect of *Anastrepha* biology that bears directly on behavior is the phenomenon of two species partitioning the same host fruit or host tree. For example, larvae of *A. sagittata*, a close relative of *A. hamata*, feed on the seeds of the yellow zapote (*Pouteria campechiana* (Kunth) Bachni, while the pulp of the same fruit is used as a food source by larvae of *A. serpentina* (Baker et al. 1944). In the case of *A. striata* and *A. fraterculus*, two species that can also be found infesting the same fruit in the same tree (guava), there is evidence of a different type of resource partitioning. In this case, fruit in certain sectors of the tree crown are preferentially infested by one species, while the rest is infested by the other (M. Aluja, M. López, and J. Sivinski, unpublished data).

Other life history characteristics of *Anastrepha* species are highly variable. For example, life expectancy among *A. ludens*, *A. serpentina*, *A. crebra* Stone, and *A. bezzii* differs sharply. When adult *A. ludens* and *A. serpentina* were kept in 30-cc Plexiglas cages under laboratory conditions, 3.3 and 8.3%, respectively, were alive after 120 days (see Jácome, 1995, for detailed methodology). In contrast, when *A. crebra* and *A. bezzii* adults were maintained in exactly the same conditions, 60 and 46.6%, respectively, were alive after 120 days (M. Aluja, unpublished data). This may be related to the fact that both *A. crebra* and *A. bezzii* are monophagous, apparently univoltine species whose adults must survive for long periods to cope with the high environmental variability, which in turn determines the fruit production schedule of their host plants, *Quararibea funebris* (Llave) Vischer and *Sterculia apetala* (Jacq.) Karst. for *A. crebra* and *A. bezzii*, respectively. *Anastrepha ludens* and *A. serpentina*, on the other hand, are multivoltine, polyphagous species, which exploit a series of host species that appear in a progressive fashion throughout most of the year. Therefore, adults of multivoltine species do not need to survive for as long as univoltine species, whose hosts are available only once a year for a few weeks. Consistent with this, we note that the maximum longevity recorded for an adult *Anastrepha* individual, kept under laboratory conditions, is 431 days (M. Aluja and I. Jácome, unpublished data). This age was attained by a male of *A. alveata*, which is monophagous. An alternative strategy, allowing flies to survive periods during which host fruits are scarce or not available, would be entering diapause. Interestingly, diapause has never been documented in *Anastrepha*, even though the phenomenon appears to be widespread among the native parasitoids attacking many species in this genus (Aluja et al. 1998a).

15.4 DIEL RHYTHMS OF ACTIVITY

15.4.1 LARVAE

Diel larval activity patterns inside a fruit have been studied only in *A. suspensa*. Larvae of this species have been shown to feed within fruit continuously over a 24-h period (Webb and Landolt 1984). When larvae are ready to exit the fruit for pupation (after completing their development), they do so by following a distinct diel pattern. In the few species studied so far, this happens in late night or early morning hours. In *A. ludens*, 92% of all larvae exited before 0900 hours (McPhail and Bliss 1933). For *A. serpentina* and *A. striata*, the peak exit period was between 0600 and 0800 hours (M. Aluja, unpublished data). Emergence from fruit is stimulated by ambient temperature, rainfall, and by the impact of fruit falling from the tree (McPhail and Bliss 1933; Darby and Knapp 1934).

Exiting fruit during late night–early morning hours may be related both to danger of desiccation and predation and to ease of soil penetration. During that time, air humidity is close to 100% and

there is no direct sunlight. Larvae crawling out of a fruit to bury themselves in the ground are thus at no risk of desiccation. Furthermore, because of damp air and soil conditions, burying procedures are greatly facilitated (reducing the risk of predation).

15.4.2 ADULTS

Despite the fact that there are clearly identifiable patterns of activity according to species, *Anastrepha* adults, in general, exhibit a high degree of plasticity in relation to most daily activities (e.g., time of day during which eggs are laid). Factors such as temperature, air humidity, or barometric pressure can influence the onset of a particular behavior. To illustrate this, *A. obliqua* adults observed in a mixed tropical plum (*Spondias purpurea* L.)/mango (*M. indica*) orchard in central Veracruz, Mexico oviposited during morning and afternoon hours, but never during midday hours (1100 to 1300). When individuals of the same population were forced to cope with different ecological conditions (i.e., cooler, wetter climate), females oviposited during the precise hours (1100 to 1500) they had avoided in a hotter and drier climate (details in Aluja and Birke 1993).

15.4.2.1 Adult Emergence

There are very few studies reporting adult emergence patterns. It appears that emergence in most species takes place preferentially during morning hours. For example, 95.7 and 62% of all *A. ludens* and *A. striata* adults, respectively, emerged between 0600 to 1000 and 0900 to 1200 hours (McPhail and Bliss 1933; Aluja et al. 1993). In contrast, Santos et al. (1993) reported that most *A. bezzii* adults emerged between 1500 and 1800 hours. Exposure to sunlight and higher temperatures appears to stimulate emergence (McPhail and Bliss 1933). *Anastrepha striata* adults remained motionless immediately after emerging, until their wings expanded and dried out and they were able to fly. They then flew to a shaded area in a tree and remained motionless for most of the day on the underside of leaves (Aluja et al. 1993). In *A. serpentina*, flies emerging from under *Manilkara zapota* (L.) P. Royen trees flew to neighboring nonhost citrus trees, where they rested for the entire day (M. Aluja, unpublished data).

Daily calling, oviposition, feeding, and resting rhythms exhibited by the few species of *Anastrepha* studied to date will be described when each of these behaviors is analyzed in depth.

15.5 TRIVIAL MOVEMENTS

15.5.1 LARVAE

Initial movements by newly hatched larvae are within a range of millimeters. As they grow, and food resources within the vicinity are depleted, larvae start to cover distances of centimeters. For example, when infesting citrus, *A. suspensa* larvae hatch in the flavedo (where eggs are deposited) and move to the albedo and pulp as they grow and the fruit ripens (Calkins and Webb 1988). The movement rate of larvae within the fruit can increase if the presence of parasitoids is detected. Larvae usually try to escape by wiggling movements or by burying themselves as deep as possible in the pulp (M. Aluja, personal observation). On occasion, third instar larvae drill a hole all the way to the surface of a fruit, extend the anterior of their bodies out of the fruit, and then crawl back into the fruit, either using the same gallery or a new one (A. Rangel and L. de la Barrera in Herrera 1905; Crawford 1918; 1927). The holes on the epidermis of the fruit are sometimes mistakenly used as evidence that the larvae have already exited the fruit, but often they are still feeding inside. It is possible that these galleries and holes are drilled to permit gas exchange. It is common to find rotting fruit where all larvae have died inside. Invariably, these fruits had no "respiration holes" and this may have resulted in noxious gases reaching lethal levels inside the fruit. It must be noted, however, that the larvae of some species do indeed exit the fruit while it is still hanging in the tree. For example, larvae of *A. hamata*, which feed exclusively on seeds, leave the fruit at a time when it is still unripe. They do so by biting their way through the hard pulp and jumping to the ground from heights of up to 10 m

(F. Díaz-Fleischer, personal observation). The only evidence of the former presence of the larvae is the exit hole around which callous tissue forms (Color Figure 14C*).

Once the fruit falls to the ground, larvae crawl out of it and bury themselves in the soil for pupation. Some do it right away, but some keep feeding and exit the fruit up to a month after it falls to the ground (Crawford 1918; 1927). Most commonly, larvae drill an exit hole in the part of the fruit touching the soil (where a humid microclimate forms because of the juices flowing). They usually pupate at a depth of 2 to 4 cm, depending on soil type and humidity (Bressan and Teles 1990; Salles and Carvalho 1993; Hennessey 1994; Hodgson et al. 1998). There are several factors that can modify this typical larval behavior. If the temperature rises to high levels in exposed fruit, larvae may crawl out and jump to the ground from heights of several meters (M. Aluja, personal observation). Despite the danger of desiccation (falling in an exposed spot with compacted soil) or predation (ants) the chances of such larvae surviving may be higher than if they remained in the fruit. Another factor that alters larval behavior is parasitism. Parasitized larvae bury themselves and pupate much faster (up to 12 h) than when unparasitized (Córdoba 1999).

15.5.2 ADULTS

As mentioned previously when discussing the behavior of teneral *A. striata* and *A. serpentina* individuals, when an adult emerges it flies to a densely foliated tree in a neighboring location and rests. Movements are circumscribed to a small area (e.g., natural patch of trees or section of orchard) and involve foraging for food and shelter/resting sites (Aluja 1993a). Mature males visit lek sites (e.g., *A. obliqua*) or patrol fruit (e.g., *A. bistrigata* Bezzi, in which males defend female resources). Females, after mating, search for suitable oviposition sites. Malavasi et al. (1983) reported high mobility of *A. fraterculus* adults between and within 11 host and nonhost trees in approximately 100 m² in Brazil. Male calling took place on nonhosts as well as hosts, but all observed mating pairs were located near the top of a tall nonhost tree. Feeding and oviposition occurred only in host trees. Resting took place on the bottom surface of leaves near the tops of host and nonhost trees. Flies moved toward the tops of trees at dusk, where they remained until the next day. When *A. obliqua* was studied in an orchard in which mango trees were surrounded by tropical plum trees (*S. purpurea*), Aluja and Birke (1993) reported that females used plum trees for feeding and oviposition, whereas males used them only for feeding. In contrast, females used mango trees principally for resting and feeding and males for sexual activities and resting. Flies moved back and forth between microhabitats, especially during early morning and late afternoon. Once all plums and mangoes had fallen to the ground or were harvested, *A. obliqua* adults started to show up in a neighboring chico zapote (*M. zapota*) orchard. There they used ripe fruit as food sources and some interspersed citrus trees as resting and male calling sites. A detailed analysis of the genetic structure of *A. obliqua* adults collected in plum, mango, chico zapote and citrus trees revealed no significant differences (B. McPherson, J. Piñero, and M. Aluja, unpublished data). This lends support to the hypothesis that members of a population actively move within an area using all available resources.

From the above, it is clear that *Anastrepha* adults readily move within a patch or orchard, but do not leave this patch if resources are plentiful. The contrary is true if the environment is unfavorable. In a series of release–recapture studies it was shown that the mobility of *A. ludens* and *A. fraterculus* was low if released in a place where vegetation, food, water, and oviposition substrates were plentiful (Plummer et al. 1941; Bressan and Teles 1991). In contrast, if flies of the same species are released in an unfavorable environment where conditions are dry, and there is a lack of host plants or adult food, they will quickly leave the release site (Shaw et al. 1967; Enkerlin 1987). Baker and Chan (1991a,b) and Baker et al. (1986) showed that wind affects the displacements of *A. ludens* and *A. obliqua* adults (i.e., mean fly movements were oriented in the direction of the prevailing wind). *Anastrepha ludens* has been reported to be able to move over remarkable distances.

* Color Figures follow p. 204.

For example, Christenson and Foote (1960) reported that individuals of this species flew approximately 135 km from breeding sites in Mexico to invade citrus groves in neighboring Texas. Shaw et al. (1967) trapped tepa-sterilized individuals of the same species up to 36 km from their release site. We believe that these long displacements were probably wind aided.

15.6 FEEDING BEHAVIOR

Feeding behavior in *Anastrepha* involves several modalities that are identical to those observed in other tephritid species such as *Rhagoletis pomonella* (Walsh) (Hendrichs et al. 1992; 1993) and *Ceratitis capitata* (Wiedemann) (Hendrichs et al. 1991): dabbing (grazing *sensu* Hendrichs et al. 1992), sucking, bubbling, and regurgitation. These behaviors were defined by Aluja et al. (1993). Dabbing is a "repetitive lowering of the proboscis to touch the surface on which the fly was feeding (usually a leaf) or while walking at increased rates of turning." This behavior has been studied in detail in *R. pomonella* by Hendrichs et al. (1992), who determined that adult flies could accrue small amounts of certain proteins and carbohydrates by grazing on leaf surfaces. Plants release such nutrients through leaching and guttation processes. Sucking "is the action of extending the proboscis to absorb liquids oozing from a fruit, water drops, or fresh bird feces" (Color Figure 1*). Bubbling is the "formation of a drop of liquid, of varying sizes, at the tip of the proboscis while the fly is sitting motionless" (Color Figure 4*). Regurgitation is the "deposition of a series of regurgitated drops on a leaf or fruit and reabsorption (reingestion) of those drops after varying intervals of time" (Color Figure 3*). Regurgitation behavior has been reported in *A. bistrigata*, *A. fraterculus*, *A. grandis*, *A. sororcula* Zucchi (Solferini 1990), *A. obliqua*, *A. serpentina*, *A. striata* (Aluja et al. 1989; 1993; Solferini 1990), *A. ludens* (Aluja et al. 1989), and *A. suspensa* (Hendrichs 1986). In the only study on *Anastrepha* where this behavior was quantified, Aluja et al. (1993), working with *A. striata*, determined that individuals deposit and reingest 23.5 drops within 12 min on the average. We believe that the number of drops depends on the type of food ingested. If it is high in water content, the number of drops should increase if flies are able to evaporate excess water from their food through regurgitation (Aluja et al. 1989). Alternatively, Drew et al. (1983) argued that through regurgitation, flies in the genus *Bactrocera* collect vital bacteria as an important source of protein. For a more wide-ranging outlook on fruit fly-bacteria relationships, see Drew and Lloyd (1991).

The few systematic studies carried out to date on feeding rhythms report varying patterns of feeding, depending on species and environmental conditions. For example, *A. suspensa* feeds throughout the day, but preferentially in the morning (Landolt and Davis-Hernández 1993). When *A. obliqua* was observed in an orchard where temperatures reached 45°C in unshaded areas, feeding followed a bimodal pattern with the most activity in the cooler afternoon hours (Aluja and Birke 1993). Feeding in the morning was mainly by females. Similar sexual differences in diel patterns of activities have been reported in other tephritids (e.g., *C. capitata*; Hendrichs and Hendrichs 1990; Hendrichs et al. 1991). Importantly, under a different set of environmental conditions (orchard in which temperature fluctuations were attenuated by densely foliated trees), *A. obliqua* fed principally between 1000 and 1500 hours (Aluja and Birke 1993). A similar pattern was reported by Malavasi et al. (1983) in *A. fraterculus*. Based on the above, we again underline the fact that when reporting feeding, or any other behavioral rhythm, all pertinent environmental variables should be quantified and described (e.g., barometric pressure, daily pattern of air temperature and humidity, light intensity, distribution and architecture of vegetation).

Anastrepha serpentina individuals fed for less than 5% of the 456 h of observation (M. Aluja and I. Jácome, unpublished data). Furthermore, an individual *A. serpentina* does not feed every day. In 39 days of uninterrupted observation, a typical *A. serpentina* individual provided with sugar, protein, and water *ad libitum* did not feed on 10 of the 39 days and fed minimally on 8 of the 39 days. Interestingly, if given a choice, most females tend to prefer sugar (sucrose) over protein or an open fruit. This "junk food syndrome" is described and discussed in detail in Jácome et al. (1999).

* Color Figures follow p. 204.

15.7 OVIPOSITION BEHAVIOR

Oviposition behavior of flies in the genus *Anastrepha* and in the closely related genus *Toxotrypana* follows a stereotyped pattern that includes the following steps: arrival on fruit (by flight or occasionally by walking), examination, and aculeus insertion (including superficial probing and actual skin puncture) (Barros et al. 1983; Landolt and Reed 1990). If an egg is laid, aculeus dragging invariably follows in species that mark. We note that this behavior (i.e., host marking) is only observed in *Anastrepha* (not in *Toxotrypana*). Examination involves moving in a straight or zigzag line on the surface of a fruit, while at the same time head-butting (bobbing *sensu* Landolt and Reed 1990) the surface. If a potential site for ovipositor insertion is detected, the speed of walking is reduced while head-butting periodicity is increased. Usually the turning angle becomes sharper, causing the fly to remain in the vicinity of the preselected site (movement in circular fashion). In *A. ludens*, the aculeus of the ovipositor is extruded at this stage, followed by aculeus insertion after movement has been completely halted (Color Figure 15*). The fly lifts its hind legs and abdomen, and inserts its aculeus at an angle of approximately 45° (Figure 15.1) (Color Figure 15A*). The probability of aculeus insertion after landing on a fruit depends on several factors: host type (primary vs. secondary), quality of fruit (e.g., degree of ripeness), and evidence of previous use by conspecifics (presence of host-marking pheromone). In *A. fraterculus*, the likelihood of a female making a puncture after landing on a fruit is 70% if it is a primary host like guava (Barros 1986). If it is a secondary host like apple, the likelihood drops to 51% (Sugayama et al. 1997). Flies invariably drag their aculeus after it is removed from the fruit flesh following release of eggs (Color Figure 15D*). An interesting facet of *Anastrepha* oviposition behavior is the fact that at least in *A. suspensa*, females are able to detect acoustical cues emitted by feeding larvae, and as a result, reject fruits that are infested (Sivinski 1987).

As noted before, ovipositional activities are greatly influenced by environmental conditions, especially ambient temperature. Despite this, overall patterns are still discernible. *Anastrepha ludens*, for example, prefers to oviposit between 1100 and 1400 hours (Birke 1995). In comparison, *A. obliqua* starts to oviposit much earlier (0700 hours) (Aluja and Birke 1993) and *A. serpentina* a little later (1200 hours) (M. Aluja, unpublished data). Oviposition behavior in *A. striata* follows a clear bell-shaped pattern beginning at 0800, ending at 1600, with a peak between 1200 and 1300 hours (Aluja et al. 1993). In the case of *A. hamata* and *A. fraterculus*, peak oviposition activity is observed at 1200 and between 1600 and 1700 hours, respectively (F. Díaz-Fleischer, unpublished data; Silva 1991; Sugayama et al. 1997).

Host-marking behavior (deposition of an oviposition-detering pheromone through aculeus dragging after laying an egg; Figure 16*) has been reported in the following *Anastrepha* species: *bistrigata* (Selivon 1991), *fraterculus* (Prokopy et al. 1982), *grandis* (Silva 1991; Silva and Malavasi 1993), *ludens* (Papaj and Aluja 1993), *obliqua* (Aluja et al. 1998b), *pseudoparallela* (Loew) (Polloni and Silva 1987), *serpentina* (Aluja et al. 1998b), *sororcula* (Simoes et al. 1978), *striata* (Aluja et al. 1993), and *suspensa* (Prokopy et al. 1977). We have further evidence that *A. alveata*, *A. leptozona*, *A. acris*, and *A. spatulata* also exhibit host-marking behavior (M. Aluja, I. Jácome, C. Miguel, and M. López, unpublished data). Importantly, field and field-cage observations demonstrated that *A. cordata* and *A. hamata* do not exhibit host-marking behavior (M. Aluja and F. Díaz-Fleischer, unpublished data). These two species are considered primitive within *Anastrepha* (Norrbom et al., Chapter 12; McPherson et al., Chapter 13). In both cases, females lay eggs in fruit that release latex after being punctured (Color Figures 12 and 14A*). Interestingly, when observing *A. cordata* oviposition behavior in *Tabernaemontana alba* Mill. (Apocynaceae), we noted that females preferentially inserted their aculeus along the middle rib of the fruit. If the process of aculeus insertion/removal lasted less than 2 min, a drop of latex covered the site of insertion. If the oviposition bout lasted longer than 2 min, we never observed the formation of a latex drop at the site of ovipositor insertion. This led us to speculate that the female, while probing, is actually trying to circumvent latex channels in the fruit or is "milking" the fruit to force release of troublesome

* Color Figures and Figure 16 follow p. 204.

latex. Our hypothesis is based on the behavior exhibited by some caterpillars which bite leaves to cause latex flow and to facilitate ingestion of leaf material (Dillon et al. 1983). Because these two primitive *Anastrepha* species, together with the closely related species *T. curvicauda*, do not mark fruit after egg laying, we feel warranted to hypothesize that host marking could be a derived behavior in *Anastrepha* (for an in-depth analysis on the evolution of tephritid host-marking behavior, see Díaz-Fleischer et al., Chapter 30). Interestingly, all three species mentioned above lay their eggs in the developing seeds of the fruit or in the fruit cavity containing seeds (*T. curvicauda*), with larvae feeding on the seeds, not the pulp (Color Figures 14B, C*). The hosts of these species all release latex after being punctured. When *A. cordata* females remove their aculeus from the fruit, they immediately try to clean it. As part of the process, they rub the aculeus tip with their legs and occasionally "rub" it against the surface of the fruit (M. Aluja, personal observation). This would support the hypothesis of Fitt (1984) that aculeus dragging is an elaboration of cleaning behavior. During such a process feces and other digestive by-products are also deposited on the surface of the fruit. It is easy to envision how such a mechanism could have evolved into what we currently know as host-marking behavior. In this respect, it is interesting to note that *A. serpentina*, a species with larvae that occasionally feed on seeds and adults that exhibit host-marking behavior, uses hosts that release latex after puncture (several plants in the family Sapotaceae). It is possible that this species represents a transition in the evolution from seed feeding, nonhost marking to pulp feeding and host marking.

As discussed earlier, it is noteworthy that two species of *Anastrepha* can utilize the same host without competition. Larvae of *A. sagittata* and *A. serpentina* feed on the seeds and the pulp, respectively, of *Pouteria campechiana*. It may be that the mark of latex left by the female ovipositing deep in the pulp to reach the young seed is a sufficient signal to another conspecific female, whereas the female laying eggs in a maturing fruit with less latex must also mark with a pheromone to signal previous occupation. Also, seeds in an optimal stage for oviposition are highly ephemeral. In contrast, larvae in pulp are exposed to more competition. Since pulp is a less ephemeral resource, it needs to be protected for longer periods.

Finally, and as also mentioned before, some *Anastrepha* species compete for the same resource. For example, *A. fraterculus* and *A. striata* both infest *Psidium guajava* L. and individuals of both species can be found in a single fruit. The same can be true for *A. ludens* and *A. obliqua* infesting *Mangifera indica*. All of these species deposit a host-marking pheromone. In such direct competition, cross species recognition of the marking pheromone is critical for the survival of the larvae. Furthermore, simultaneous infestations of the same fruit by species in two genera (*A. fraterculus* and *C. capitata*) have been reported for peach, apple, and coffee in Brazil (Pavan and Souza 1979). *Ceratitis capitata* is an exotic species that was introduced in Brazil from either the Mediterranean area or the African continent in 1901 (Ihering 1901). Aluja et al. (1998b) have shown that *Anastrepha* individuals cannot recognize the host-marking pheromone (HMP) of *C. capitata* and, as a result, direct competition is unavoidable. It would be interesting to follow the probable development of intergeneric recognition of the HMP into the next century.

When comparing oviposition behavior among *Anastrepha* species, we have arbitrarily created four groups based on their clutch size: always one egg (e.g., *A. obliqua*; Celedonio-Hurtado et al. 1988), small (one to three eggs; e.g., *A. striata*; Aluja et al. 1993), medium-sized (1 to 40 eggs; e.g., *A. serpentina* and *A. ludens*; Jácome 1995 and Dávila 1995, respectively), and large clutches (>30 eggs; e.g., *A. grandis* and *A. bezzii*, Silva 1991 and M. Aluja and I. Jácome, unpublished data, respectively). Clutches of up to 110 eggs have been reported for *A. grandis* (Silva 1991). Importantly, even in clutch-laying species, ovipositing only one egg is also common. In studies aimed at determining the effect of adult diet on the basic demographic parameters of *A. serpentina* and *A. ludens*, it was determined that these species lay 1 to 19 and 1 to 23 eggs/clutch, respectively (Jácome 1995; Dávila 1995). Oviposition substrates used were 3-cm-diameter agar spheres wrapped in Parafilm (details of methodology in Boller 1968). *Anastrepha ludens* that were fed on sucrose and protein produced average clutch sizes of 3.96 ± 0.3 ($N = 264$; measurement of variance is S.E.; Dávila 1995).

* Color Figures follow p. 204.

In a much earlier study with the same species, McPhail and Bliss (1933) reported an average clutch of 5.4 ± 0.2 (range = 1 to 18), with flies spending 1 to 12 min per oviposition bout.

Berrigan et al. (1988) argued that clutch size in *A. ludens* was largely determined by host size and variation among females, ranging between 1 and 40 eggs/clutch. Host color, host density, fly density, and fly age did not affect clutch size. Average clutch size was 4.4 eggs and 12.7 eggs in 2-cm- and 11-cm-diameter artificial hosts, respectively. These authors report that in no-choice experiments, the increase in clutch size with increased host size appeared to peak at a host size of ~7 cm.

When analyzing the evolution of clutch size, one should take into account that most wild host fruits of *Anastrepha* tend to be small (3 to 30 g) (López et al. 1999) and that one or few eggs are laid in them. We thus believe that the large clutch sizes seen in some *Anastrepha* species of economic importance (e.g., *A. ludens*, *A. serpentina*, *A. grandis*) could be a recent development related to the appearance of artificially large, cultivated fruit. *Anastrepha ludens* coexisted for a long time with the host *S. greggii*, whose fruit weighs approximately 2 to 3 g and can only harbor one or two larvae (Plummer et al. 1941). In contrast, the commercial Marsh grapefruit commonly infested by *A. ludens* larvae weighs an average of 312 g (range = 150 to 800 g) (López et al. 1999) and can easily harbor more than 80 larvae. It would be interesting to ascertain clutch size in *A. ludens* populations that have not been in contact with cultivated plants (possibly in remote canyons in the states of Nuevo León and Sinaloa, Mexico).

15.8 MATING BEHAVIOR

The sexual behaviors of a handful of *Anastrepha*, mostly economically important species, have been examined in detail (Aluja 1994). Because some of these species (e.g., *A. suspensa*, *A. ludens*, and *A. obliqua*) have been mass-reared for sterile male releases, it has been necessary to understand male-male competitive interactions and female mate-choice criteria so that quality control measures could be instituted and trapping done more effectively (e.g., Burk 1986; Moreno et al. 1991; Mangan et al. 1992). Since pestiferous, polyphagous species have attracted a disproportionate amount of research, the behaviors reviewed below may not be representative of the genus as a whole.

In general, the known mating systems of *Anastrepha* species are complex and often include male territories (often aggregated in some degree to form leks), male pheromone emissions from pleural glands and evaginated anal membranes (Color Figure 7A*), pheromone depositions on leaves (Color Figure 7B*), wing fanning-acoustic signals (songs) produced both prior to and during coupling, wing motions (semaphoring) accompanied by "graceful" sideways-arching body movements, and extensions of the male mouthparts and other activities during copulation (see Sivinski et al. 1984; Sivinski and Burk 1989) (Color Figure 8*). Some species perform additional behaviors such as trophallaxis (the female consumption of fluids provided by the male; Aluja et al. 1993) (Color Figure 9*) and short looping flights over leaf territories (Aluja 1993b). Copulation durations vary with species and may serve as a means of preventing subsequent reinseminations by sexual rivals or as a means of transferring male material investments to mates or zygotes (see Alcock 1994). The evolution of sexual behavior, both in *Anastrepha* and other fruit flies, is considered in Sivinski et al. (Chapter 28).

15.8.1 MATE ACQUISITION STRATEGIES

In broad terms, two mating strategies have been reported in *Anastrepha*: (1) resource defense by which males patrol and defend clumps of fruit that are attractive to receptive females (to date only reported in one monophagous species: *A. bistrigata*, Morgante et al. 1993) and (2) lek polygyny, which appears to be the norm in *Anastrepha*. Of the latter system there seem to be gradients as will be discussed later. In the case of leks, females visit these calling arenas, devoid of any resource, and actively choose a mating partner (see reviews by Burk 1983 and Hendrichs 1986).

Mating occurs on the leaves or leaf nodes (rarely on fruits) of host trees, or occasionally on the leaves of more hospitable tree canopies adjacent to hosts (e.g., Burk 1983; Malavasi et al. 1983;

* Color Figures follow p. 204.

Aluja and Birke 1993). Males typically maintain a territory on the underside of a leaf from which they emit pheromones and produce calling songs (see below).

Male behavior of *A. suspensa* in field cages and in the field has been described in detail by Dodson (1982), Burk (1983), and Hendrichs (1986). As the late afternoon period of sexual activity approaches, males become "alert," raising themselves off the surface, holding their wings at an acute angle, and stationing themselves at the leaf base, facing the stem and often astride the main leaf vein. As time passes, they begin to semaphore (see below) and eventually to call (see below).

Territories, at least those of polyphagous species, are often aggregated to form leks (e.g., Perdomo 1974; Dodson 1982) (Color Figure 5*), although the propensity to form leks varies with species. Even in species where aggregations are common, isolated males ("satellite males") may signal and obtain mates (e.g., Sivinski 1989; Robacker et al. 1991). There is no fixed definition in the literature of what constitutes a lek in *Anastrepha* species. Although two males on adjacent leaves probably represent an interacting group (see sections on male agonistic interactions and female mate-choice criteria), Aluja and Birke (1993) defined an *Anastrepha* lek as "an aggregation of at least 3 males calling simultaneously in a clearly defined area, usually adjacent leaves of a single branch" (Color Figure 5*). The largest *A. suspensa* lek observed by Sivinski (1989) contained nine calling males, none more than 15 cm from at least one other participant. Malavasi et al. (1983), working with *A. fraterculus*, noted a lek of five males within 80 cm of one another. In *A. suspensa*, leks form in areas where males and females are also likely to be found in nonsexual situations, presumably because of favorable microhabitats. Certain leaves may be occupied by signaling males for several consecutive days (Sivinski 1989). Aggregation locations in *A. obliqua* are also influenced by microhabitat (Aluja and Birke 1993) and calling territories of *A. ludens* tend to occur in the interior half of the tree canopy (Robacker et al. 1991). There is little apparent structure to leks, although smaller males of *A. suspensa* have a tendency to be located nearer the tips of branches. This could be due to no more than the combined tendencies of larger males to defeat smaller opponents and for flies in flight to move toward better lit areas (Sivinski 1989; see, however, Hendrichs 1986; and Section 15.8.11 on female mate-choice criteria).

Not all *Anastrepha* species form leks or form them as consistently as others. *Anastrepha striata* is characterized as an intermediate lekking species because of its propensity to call alone (Aluja et al. 1993). Furthermore, *A. bistrigata* males do not appear to lek at all and maintain territories on or near fruit-oviposition sites (Morgante et al. 1993).

15.8.2 DIEL PERIODICITY

Daily rhythms in male calling vary sharply in *Anastrepha* (we only provide information on male calling, since mating is initiated at roughly the same time as calling activities take place). Its onset fluctuates from before sunrise to after sunset, depending on the species. To illustrate this, we have graphed the calling patterns exhibited by 20 *Anastrepha* and one *Toxotrypana* species (Figure 15.2).

Despite the fact that the daily pattern of calling rhythms appears to be one of the most hard-wired behaviors in *Anastrepha* (probably driven by a circadian clock; see Smith 1979 for an in-depth analysis of the phenomenon for other tephritid flies), it is also influenced by environmental conditions. As discussed by Aluja and Birke (1993), and references therein, "daily patterns of activity in insects have evolved in response to ecological factors and are strongly influenced by prevailing physical characteristics of the habitat." It is probable that selection acted upon genotypes that were more efficient at timing the broadcast of signals (e.g., pheromones, sounds) under situations such as a humid evergreen rain forest or a drier deciduous forest. For example, if temperatures are below or above the optimum (20 to 24°C), the onset of calling is delayed in *A. ludens* (M. Aluja and J. Piñero, unpublished data). A similar pattern was observed with *T. curvicauda*. Flies observed during January under cooler temperatures called much later than flies under warmer temperatures during August (see Figure 15.2; details of study in Aluja et al. 1997).

* Color Figures follow p. 204.

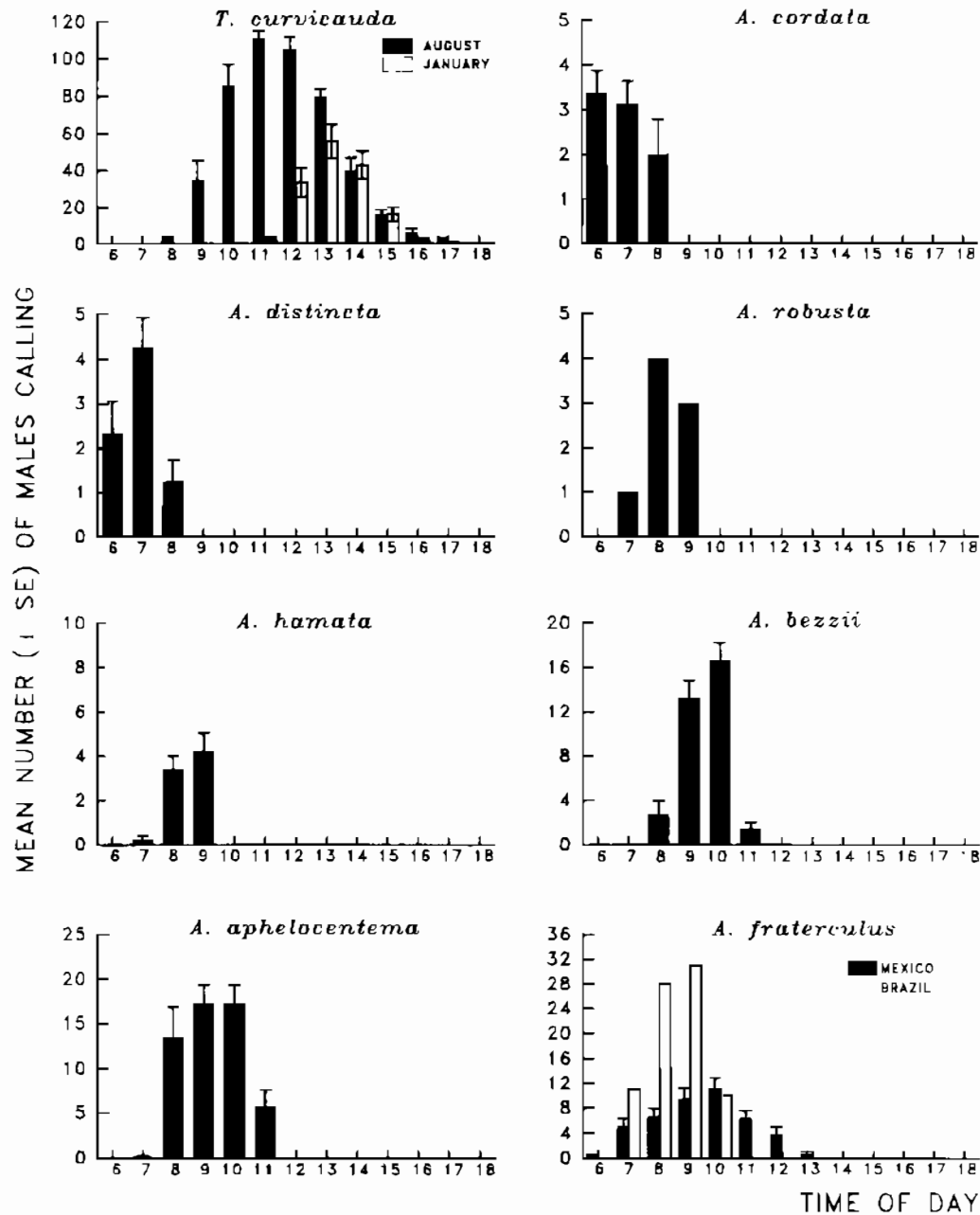


FIGURE 15.2 Distribution of calling activities in 20 *Anastrepha* species and *Toxotrypana curvicauda*. Information on *A. aceris*, *A. alveata*, *A. aphelocentema*, *A. bezzii*, *A. cordata*, *A. crebra*, *A. distincta*, *A. hamata*, *A. leptozona*, and *A. serpentina* comes from previously unpublished data by M. Aluja, I. Jácome, J. Piñero, and F. Díaz-Fleischer (methodology used to conduct these observations is described in detail in Aluja et al. 1993). Information on the remaining species comes from *A. histrigata* (Selivon 1991), *A. fraterculus* (Malavasi et al. 1983; M. Aluja, J. Piñero, V. Hernández, and B. McPherson, unpublished data), *A. grandis* (Silva 1991), *A. ludens* (McPhail and Bliss 1933; Aluja et al. 1983), *A. obliqua* (Aluja et al. 1993), *A. pseudoparallela* (Polloni and Silva 1987), *A. robusta* (Aluja 1993b), *A. spanulata* (M. Aluja and M. López, unpublished data), *A. suspensa* (Hendrichs 1986), *A. striata* (Aluja et al. 1993), and *T. curvicauda* (Aluja et al. 1997).

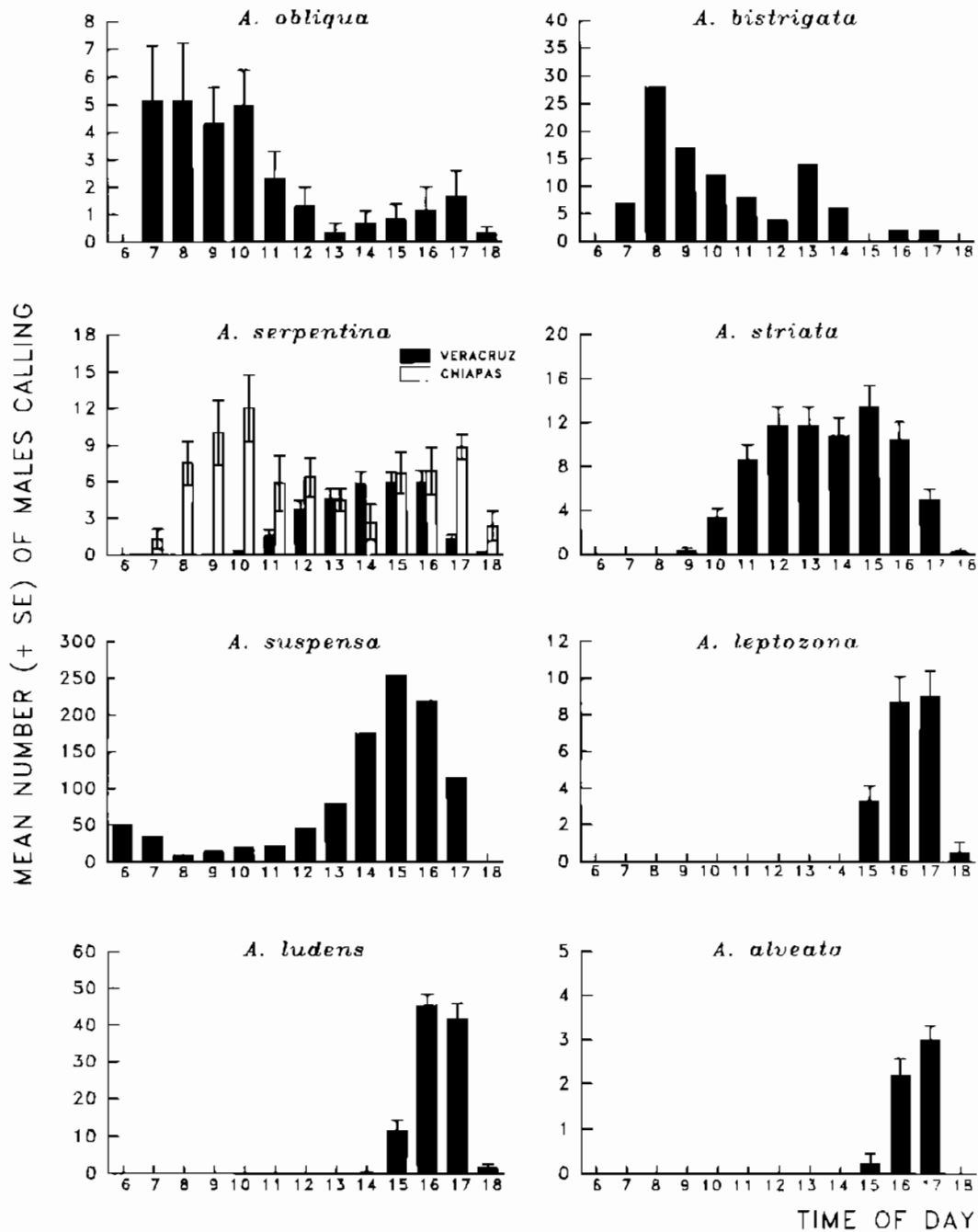


FIGURE 15.2 (continued)

Despite the fact that temperature can delay or push forward the onset of calling, we believe that the most critical extrinsic factor regulating calling (mating) behavior in *Anastrepha* is light intensity. F. López and R.H. Rhode (work reviewed by McFadden 1964) conducted a series of experiments on the effect of photoperiod and wavelength on the mating of *A. ludens*. These authors found that

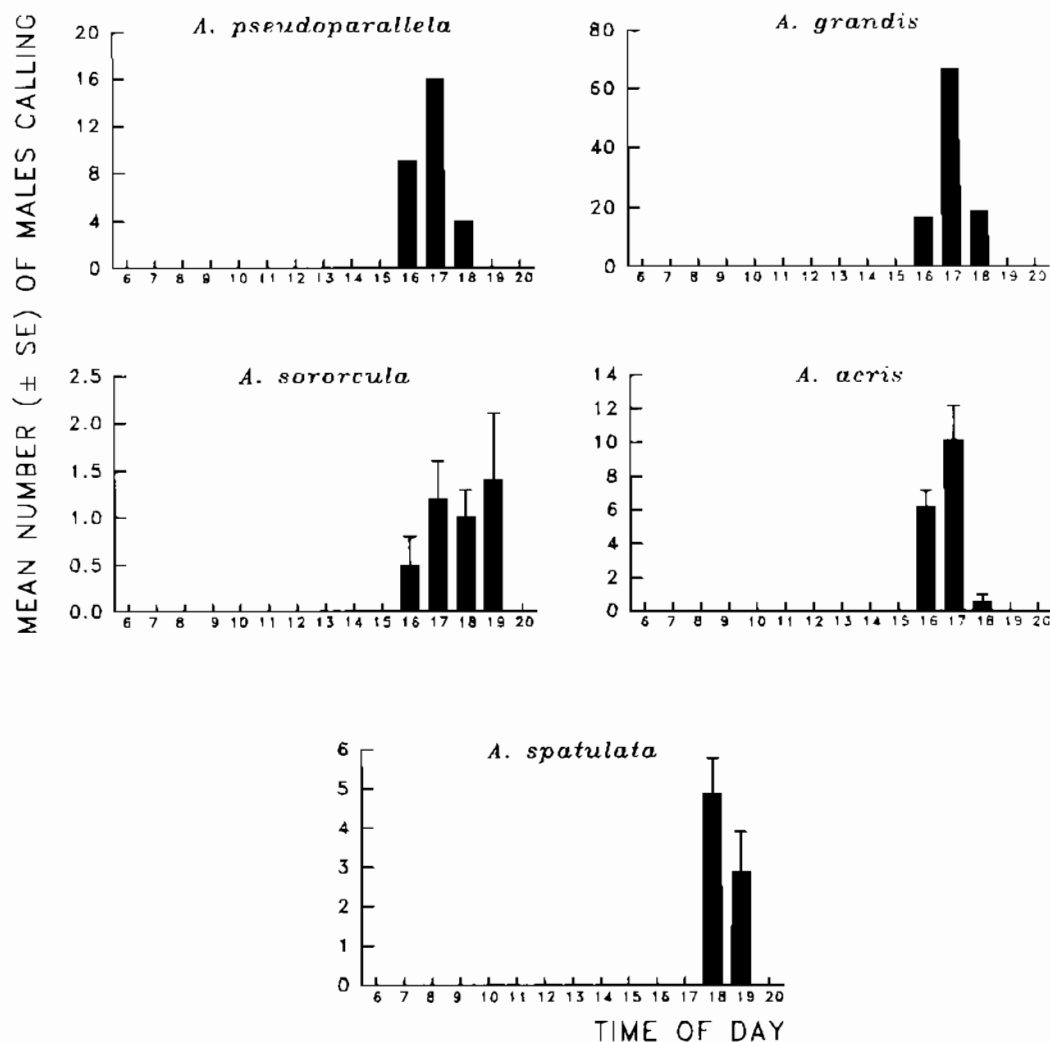


FIGURE 15.2 (continued)

under natural light conditions in the laboratory, caged *A. ludens* individuals began mating in midafternoon with a peak occurring between 1600 and 1800 hours. By varying this normal pattern under controlled conditions, flies could be induced to initiate mating during the midmorning hours and to reach a peak at 13:00 hours. In nature, *A. ludens* males only call in late afternoon (dusk) when light intensity is low (4 to 6 footcandles) (McPhail and Bliss 1933; Aluja et al. 1983).

Furthermore, there seem to be populational differences with respect to calling rhythms. In Figure 15.2, we describe the daily calling rhythm of *A. serpentina* cohorts stemming from two localities in Mexico separated by ~1200 km: the states of Veracruz (Apazapan) and Chiapas (Tapachula). Note that, unlike the Veracruz population, individuals from the Chiapas population had a much more extended calling period that included morning hours. A similar pattern is observed when analyzing calling rhythms of *A. fraterculus* populations in Mexico and Brazil (Figure 15.2). We currently lack enough information to interpret these variations in calling rhythms adequately. We could be dealing with biotypes adapted to local environmental conditions or with an unresolved species complex.

15.8.3 MALE AGONISTIC INTERACTIONS

Lekking insects, such as many *Anastrepha* species, interact in three ways (Thornhill and Alcock 1983): (1) they are attracted to the sexual signals of other males (see Heath et al., Chapter 29); (2) they participate in signaling interactions such as mutual stimulation; and (3) they engage in aggressive interactions for the possession of territories (example of aggressive interaction in lek of *C. capitata* in Color Figure 11*).

Anastrepha suspensa males placed in the presence of other males begin pheromone signaling more quickly (have a shorter latency) than those maintained alone (Burk 1984). Male reactions to intruders consist of lowering the body to the leaf surface, pressing the wings against the side of the body, and extending the proboscis forward (the "arrowhead" posture; Dodson 1982; Burk 1983). Escalation of the confrontation leads to head butting and audible "aggression" songs produced by wing buzzing (similar behaviors have been observed in *A. ludens*; Robacker and Hart 1985; see below).

Resident males in wild populations of *A. ludens*, *A. obliqua*, and *A. suspensa* were usually able to defend their leaf territories against aggressive interlopers (Aluja et al. 1983; Burk 1983). In laboratory experiments with *A. suspensa*, prior residence on the territory and large size characterize males that win agonistic interactions (Burk 1984). The two factors interact so that large residents are very successful against smaller interlopers, and large residents are more successful than large interlopers, but small residents often lose their territory to large interlopers.

Given the apparent importance of large size to male *A. suspensa*, both in terms of intrasexual agonistic interactions and female mate choice, it is something of a mystery that males tend to be the smaller sex; i.e., they are not as large as a fruit fly can become in that particular niche. In a field-cage study of *A. ludens* sexual behavior, there was no relationship between male size and sexual success (Robacker et al. 1991; see section on female mate-choice criteria). Nonsexual explanations for small-male sexual dimorphism in the genus are provided by Sivinski and Dodson (1992).

15.8.4 LOOPING FLIGHTS AT TERRITORIES

Male *Anastrepha* rarely leave and return to the same spot during their calling bouts. *Anastrepha robusta* and *A. leptozona* are exceptions (Aluja 1993b; M. Aluja, J. Piñero, and I. Jácome, unpublished data). *Anastrepha robusta* is a large and widely distributed species, but seldom observed. The males perform many of the behaviors common to other species of the genus, such as wing fanning (calling song), pheromone gland puffing, and touching the everted anal membrane to leaf surfaces (see relevant sections). An additional behavior is looping flights, performed repeatedly, 15 to 40 cm in distance, which depart from and return to the same leaf territory (Figure 15.3). More than 10 of these loops may be performed by an individual every minute (Aluja 1993b). In *A. leptozona*, the loops are not as wide but are also very common. Flying as a mating strategy is rare for tephritoids outside of the swarming Lonchaeidae (see Sivinski, Chapter 2).

15.8.5 PHEROMONES

As far as is known, male-produced pheromones are present in all species of *Anastrepha* (see Nation 1972, for an early report). Their production and composition is discussed by Epsky and Heath (1993) and Heath et al. (Chapter 29).

The males of many *Anastrepha* species touch their leaf territories with their evaginated anal membranes (i.e., proctiger), a structure associated with pheromone emission (e.g., Nation 1989; Aluja 1993b; Aluja and Birke 1993; Aluja et al. 1993). This behavior has been examined in *A. suspensa* (Sivinski et al. 1994). Bouts of anal touching occur while a second set of pheromone-related structures, the lateral abdominal pleural glands, are protruded. They also coincide with wing fanning, which may help disperse pheromones (see Section 15.8.6). Five of the eight components

* Color Figures follow p. 204.

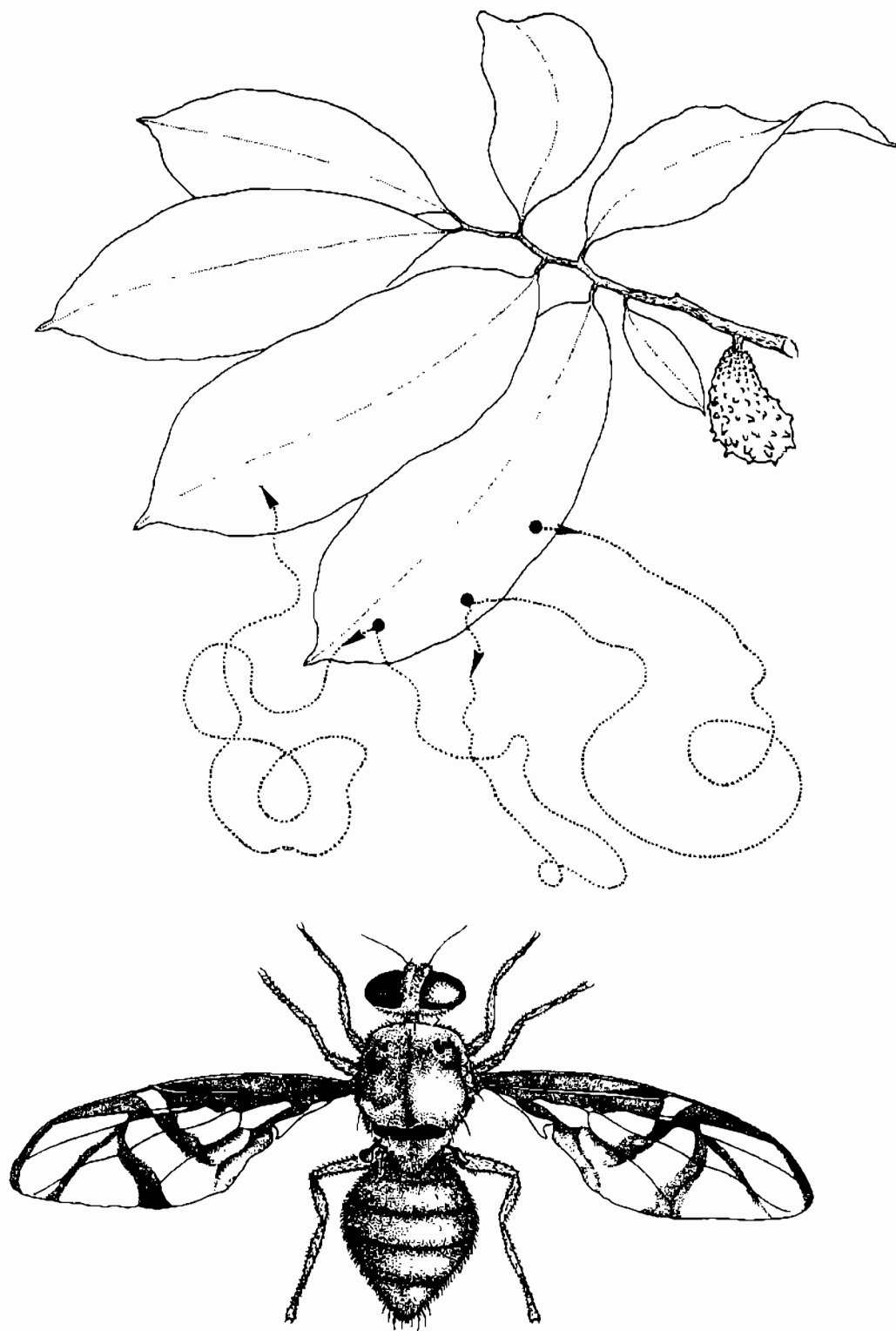


FIGURE 15.3 Graphic representation of loops performed by *A. robusta* males while calling on an *Annona muricata* L. tree. (From Aluja, M., *Fla. Entomol.* 76: 391–395, 1993. With permission.)

of *A. suspensa*'s pheromone were recovered from leaves that had previously been held as territories by signaling males. Only one component was detected on leaves that had been held near, but not in contact with, signaling males. Thus, the bulk of the pheromone chemicals on the leaves were there due to anal touching. In the laboratory, mature virgin females were more likely to be in contact with leaves that had been anal-touched by males than with untouched control leaves. There was no difference in female contacts with leaves that had been kept with sexually immature males or females and their respective controls. The ability of leaf territories to hold pheromones and apparently enhance chemical signals may increase their value to territory holders. Pheromone deposits may be one reason why aggressive interlopers would want to expel territory holders and obtain their signaling platform (see section on mating systems and Sivinski et al., Chapter 28, on the evolution of mating behavior).

Related to the anal touching (dipping) behavior observed in males of *A. suspensa* and other *Anastrepha* species, is the anal dragging behavior exhibited by *A. hamata* males (M. Aluja, personal observation). In between wing-fanning bouts, males repeatedly drag their proctiger along leaf pedicels or branchlets (Color Figure 7B*). This seems to be an elaboration of the anal touching (dipping) behavior exhibited by other *Anastrepha* species. We have not been able to ascertain if males are depositing a pheromone while dragging the proctiger, but this seems likely.

15.8.6 CALLING SONGS

The wing fanning that accompanies anal membrane touching may help disperse pheromones deposited on leaf territories; however, it also generates an acoustic "calling song" that has sexual significance and has been examined in detail in *A. suspensa* (Webb et al. 1976; also see Sivinski et al., Chapter 28). Songs are produced by males on their calling stations both in the presence and absence of other flies, although the incidence of calling and the characteristics of the song vary under different social circumstances and presence/lack of adult food and host fruit (see below; Sivinski and Webb 1986; Landolt and Sivinski 1992). Calling songs in *A. suspensa* are largely produced by wing movements, with thoracic vibration making a lesser contribution (Sivinski and Webb 1985), and generally have a fundamental frequency of 140 to 150 Hz (Webb et al. 1984; Burk and Webb 1983). The typical form of *A. suspensa*'s song is repeated episodes of wing fanning (pulse trains), each ~0.5 s long separated by ~0.5-s-long pulse-train intervals. There is a sexual dimorphism in the shape of the wings in *Anastrepha*: those of the male are more oval (Sivinski and Webb 1985). It has been suggested that this shape is an adaptation for acoustic signaling; however, there are alternative explanations based on male flight abilities (Sivinski and Dodson 1992).

Female *A. suspensa* use male songs to locate calling sites. Sticky traps baited with recorded calling songs captured more virgin females than silent controls, but the range of attraction is unknown (Webb et al. 1983).

In addition to serving as an attractant, the calling song appears to represent an important courtship component. Certain song characteristics are correlated with male size (Burk and Webb 1983). For example, in *A. suspensa*, large males tend to have a greater propensity to sing, and have songs with shorter pulse-train intervals and lower fundamental frequencies. Since females given a choice of a large and a small male prefer to mate with the larger, it is possible that females could use the size-correlated song characteristics as criteria for choosing or rejecting a courting male.

In one laboratory study, *A. suspensa* males were divided into four categories of sexual success: (1) those that mated on their first attempt; (2) those that mated after repeated attempts; (3) those that mounted but were rejected; and (4) those that never mounted a female during the 30-min observation period (Webb et al. 1984). There was only one difference in their calling songs: the bandwidth of the fundamental frequency was broader in males that never mounted a female compared with males that copulated on their first attempt. Expanded bandwidth could reflect a

* Color Figures follow p. 204

physical disability, and has been found in the acoustic signals of improperly irradiated *C. capitata* males suffering from malformed wings ("droopy-wing syndrome") (Little and Cunningham 1978).

However, in another study of *A. suspensa* female response to calling songs, there was evidence that the pulse-train interval was an important characteristic to females when choosing mates. Virgin females were more likely to react to recorded songs with short pulse-train intervals (a large-male characteristic) than to songs with long intervals (a small-male characteristic; Sivinski et al. 1984). There was no difference in the reactions of mated females, and males were most active in the periods of silence that separated the recordings.

Calling males in *A. suspensa* modify their songs in the presence of potential mates and sexual rivals by shortening the pulse-train interval when females are nearby and lengthening the pulse train when males are placed next to them (Sivinski and Webb 1986). Shortening the pulse-train interval near females is consistent with a short interval being a song characteristic that females find attractive in a mate.

The calling songs of the other species of *Anastrepha* that have been examined are similar in pulse train and pulse-train interval to those of *A. suspensa* (J. Sivinski, unpublished data). Mankin et al. (1996) compared the calling songs of *A. grandis*, *A. obliqua*, *A. sororcula*, and two populations of *A. fraterculus*. *Anastrepha grandis* had the longest pulse train and pulse-train interval, and lowest fundamental frequency. *Anastrepha fraterculus* had the shortest pulse train and pulse-train interval. However, there was no single characteristic that was unique in every species and could be used to identify a species or different populations of a species.

Importantly, there are some primitive *Anastrepha* species like *A. cordata* that do not produce any calling songs. The same is true in the case of *T. curvicauda*. In these species, males only raise their abdomen (with puffed pleural glands) but do not fan their wings. Wing fanning could be considered a derived behavior that may have evolved from aggressive male/male encounters during which individuals wing fan vigorously.

15.8.7 PRECOPULATORY SONGS

There is a second type of wing-fanning-acoustic signal performed by *Anastrepha* males, and which again has been examined in *A. suspensa*. As males mount females and attempt to insert their phallus into the ovipositor, they produce a "precopulatory song." This differs from the calling song by its continuous nature (no repeated pulse trains), its higher fundamental frequency (+19 Hz), greater energy (+199 mV under Fast Fourier Transform [FFT] curve), smaller waveform distortion (-35%), and lesser range of fundamental frequencies (-49 Hz) (Webb et al. 1984). In summary, it is a relatively pure, high, intense, and energetic sound that usually lasts until the male genitalia have begun to penetrate the female's uplifted ovipositor (~35 seconds), although particular precopulatory songs can last up to 15 min or more. Occasionally, a similar sound will be produced by copulating males in apparent response to female restlessness (i.e., females apparently do not cooperate completely with postintromission processes such as further penetration or transport of sperm). The energy invested by males in this final acoustic signal prior to insemination suggests that it is an important component of courtship that plays a critical role in maximizing male reproductive success (Eberhard 1994; 1996).

Mounted and singing males are frequently rejected by females before they can completely insert their phallus. Burk and Webb (1983) noted that males that copulated had songs that were ~10 dB more intense than those that did not copulate (dB, decibel, being a measure of sound pressure level) and were rejected, and that this difference occurred regardless of male size. Since an increase of 6 dB represents a doubling of sound output, the differences between successful and unsuccessful songs are dramatic. Webb et al. (1984) examined a larger sample of successful and unsuccessful songs and again found that successful songs had a significantly higher sound pressure level and were also more energetic, had narrower frequency bandwidths, and were less distorted. In experiments with recorded songs, muted (dealtated) males were more likely to copulate if the

correct form of the precopulatory song was broadcast in their cage at a high intensity than if the correct song was played at a low intensity or an incorrect calling song at a high intensity (Sivinski et al. 1984).

Precopulatory songs vary in different species. Descriptions of courtship in *A. sororcula* suggest a more energetic song than that produced by *A. obliqua* (Silva et al. 1985).

15.8.8 WING MOVEMENTS

Both sexes of many tephritids and species in related families move their patterned wings in a manner reminiscent of semaphoring (see Sivinski, Chapter 2, on the behaviors of related families; and Headrick and Goeden 1994, for detailed definitions of wing movement modalities). The wings may be brought forward either together (*enantion*; e.g., *A. ludens*) or alternately (*hamation*; e.g., *A. suspensa*, *A. fraterculus*; Robacker and Hart 1985; M. Aluja, unpublished data). The reason for these movements, produced by males and females, mature and immature individuals, and in both sexual and seemingly nonsexual situations, is a mystery. The energy that must go into the repeated motions suggests they have some important function, although their purpose is not necessarily communicative. For example, metabolic heat from flexing could keep flight muscles in optimal condition for escape. However, there is circumstantial evidence that at least some semaphoring has a sexual role. In *A. suspensa*, males greatly increase the rate of semaphoring in the presence of potential mates (Sivinski and Webb 1986). On the average, 35% of a courting male's time is spent in such wing movements, and this increased time investment coincides with a decline in the production of another signal, the calling song, with known sexual significance. Not all *Anastrepha* engage in semaphoring during courtship. When an *A. striata* male detects a female, he extends his proboscis and holds his wings close to his body ("arrowhead" posture described in Section 15.8.3 on male agonistic interactions; Aluja et al. 1993) (Figure 15.4).

15.8.9 TROPHALLAXIS

While examples of trophallaxis (males providing an oral substance that is consumed by females) are relatively common in the nonfrugivorous Tephritidae, there is only a single instance described for *Anastrepha* (see Chapters 2 and 28 on the evolution of mating behavior and the behaviors of related families). *Anastrepha striata* females circle in front of courting males and periodically stop to touch their labella with the extended labella of the males (Figure 15.4; Aluja et al. 1993). During these touches a substance is offered by the male that is imbibed by the female. The only other described instance of male-produced substances transferred to mates occurs in *A. suspensa*, where radioactively labeled materials in the ejaculate have been subsequently discovered in unfertilized eggs and female tissue (Sivinski and Smittle 1987). However, there is no evidence that insemination enhances female longevity or that the ejaculates of particular males (i.e., large males) increase fecundity (Sivinski 1993).

15.8.10 BEHAVIORS DURING COUPLING

In *A. ludens*, the male palpitates the vertex of the female's head and dorsal anterior thorax, while the female palpitates the substrate. The position of the legs of male *A. ludens* is as follows: foretarsi along anterior thorax of female; mesotarsi along pleural region of midabdomen of female; metatarsi along oviscape or distal portion of female's wings (Dickens et al. 1982; see copulating pair of *A. serpentina* in Color Figure 8*). Male *A. bistrigata* perform more rapid and frequent palpitations of the female's head than do male *A. obliqua* (Silva et al. 1985). In *A. obliqua*, the mounted male releases an oral fluid onto the female's head (Silva et al. 1985).

* Color Figures follow p. 204.

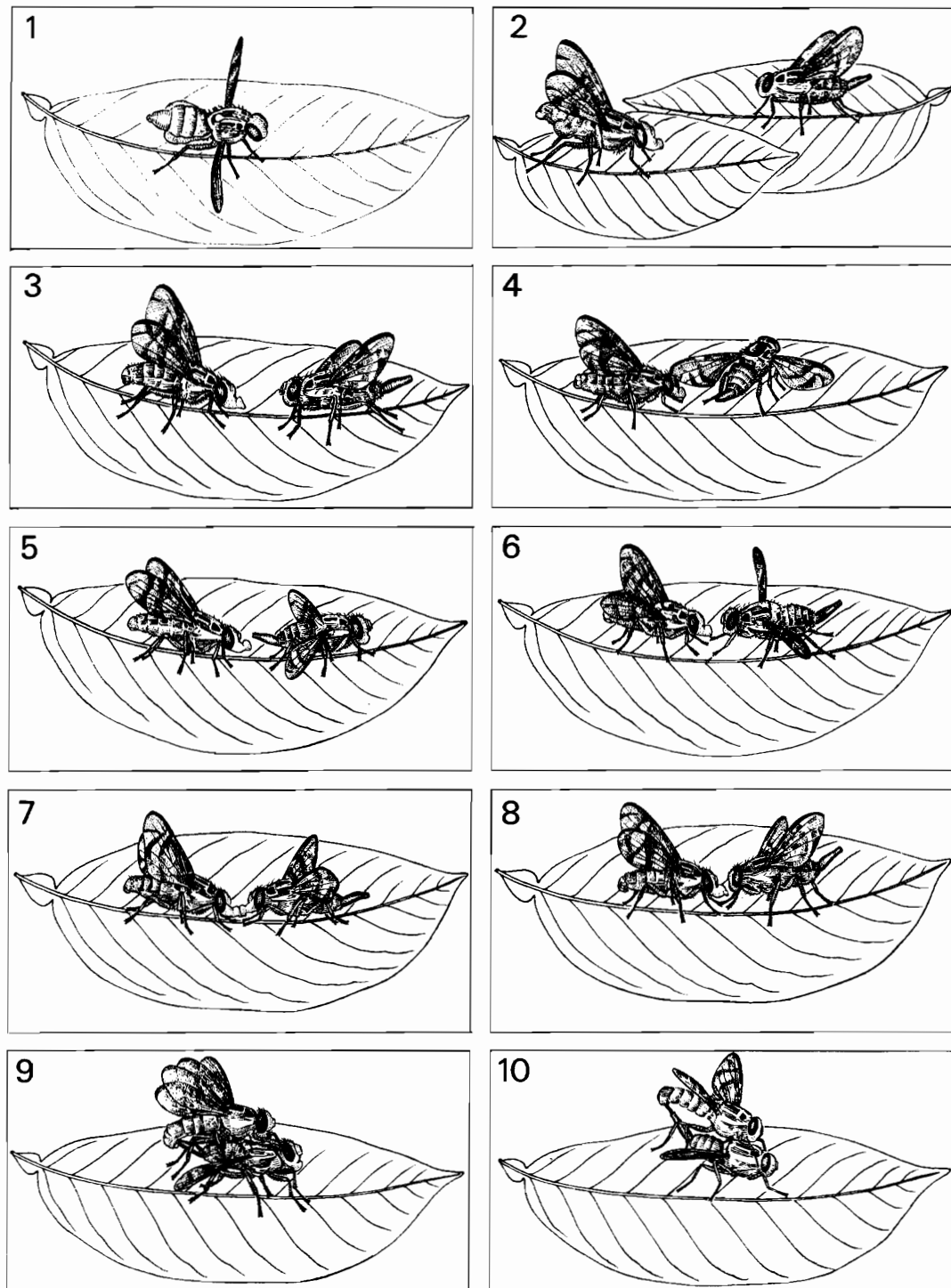


FIGURE 15.4 Typical sequence of events before and during *A. striata* pair formation and prior to copulation. Note the labella-to-labella contacts (picture 7) and the stiff position of the male while the female circles in front of him. (From Aluja, M. et al., *Ann. Entomol. Soc. Am.* 86: 776–793, 1993. With permission.)

15.8.11 FURTHER CRITERIA FOR FEMALE MATE CHOICE

When given a choice between sexually experienced and virgin males, female *A. fraterculus* overwhelmingly preferred previously mated males (De Lima et al. 1994). In *A. suspensa*, large males that would have typically been chosen as mates were temporarily less attractive following mating (the effect dissipated after 2 h; Sivinski 1984). This occurred in spite of no decrease in calling song production. Courtship in *A. striata* includes repeated attempts (mean 13.3 ± 1.9 , S.E.) by males to mount females (Aluja et al. 1993). Male persistence might be a quality solicited and then judged by choosy females (Thornhill and Alcock 1983).

In a field-cage study of *A. ludens*, four factors were positively correlated with male mating success: the number of days males survived, the tendency of a male to join a lek, the propensity to engage in fights with other males, and fighting ability (Robacker et al. 1991). All of these characteristics are related to the ability of the male to find and stay within a lek, and it is suggested that females search for areas of concentrated male activity containing highly contested leaves. By arriving at a contested leaf, females have a good chance of finding a male fit enough to have won or held its leaf during recent fighting. Most *A. ludens* matings occurred at the uppermost locations with leks (Robacker et al. 1991). Hendrichs (1986) examined the sexual behavior of *A. suspensa* in a field cage and found that males compete for leaves in the centers of aggregations and that females usually mate in the center as well. However, evidence that females make mate-choice decisions solely on the basis of male locations within leks rather than for the characteristics of particular males may be difficult to reconcile with laboratory studies that suggest individual qualities are important in mate choice.

Aluja et al. (1999) found that adult food quality affected male mating success in field-cage studies aimed at comparing the sexual behavior of *A. ludens*, *A. obliqua*, *A. serpentina*, and *A. striata*. Males that had fed on a protein-rich diet were more competitive than those that only had access to sugar. Furthermore, a poorly fed *A. striata* male that was able to copulate, considerably reduced its partner's life expectancy, fecundity, and the hatchability of the eggs produced by the mated female (Sánchez 1998). By contrast, in the case of *A. ludens*, adult diet had no effect on male mating success (Aluja et al. 1999).

15.8.12 COPULATION DURATION

Information on copula duration of 19 *Anastrepha* species is graphed in Figure 15.5. An interpretation of the tremendous range of copulation durations within this genus is offered by Sivinski et al. (Chapter 28).

15.8.13 FEMALE SEXUAL MATURATION PERIODS

In the few studied species, sexual maturation periods are: *A. serpentina* 14 days (Martínez et al. 1995), *A. striata* 14 to 15 days (Ramírez-Cruz et al. 1996), *A. fraterculus* 17 days (De Lima et al. 1994), *A. pseudoparallela* 18 days, *A. sororcula* 24 days and *A. bistrigata* 26 days (Silva et al. 1985), *A. obliqua* 7 to 19 days (Brazil; Bressan 1996) or 10 to 12 days (Mexico; M. Aluja, unpublished data), and *A. suspensa* 14 days (Dodson 1982).

15.8.14 COPULATION FREQUENCY

Comparing several *Anastrepha* species, Silva et al. (1985) found that *A. fraterculus*, *A. sororcula* and *A. pseudoparallela* females rarely mated more than once and, in one study, never more than three times. This is in contrast to *A. bistrigata* in which exceptional females mated up to 13 times (Silva et al. 1985). Laboratory-reared *A. fraterculus* females can remate up to eight times (De Lima et al. 1994). Female propensity to remate in *A. suspensa* is dependent on numerous oviposition opportunities being available, suggesting that sexual receptivity returns with the exhaustion of

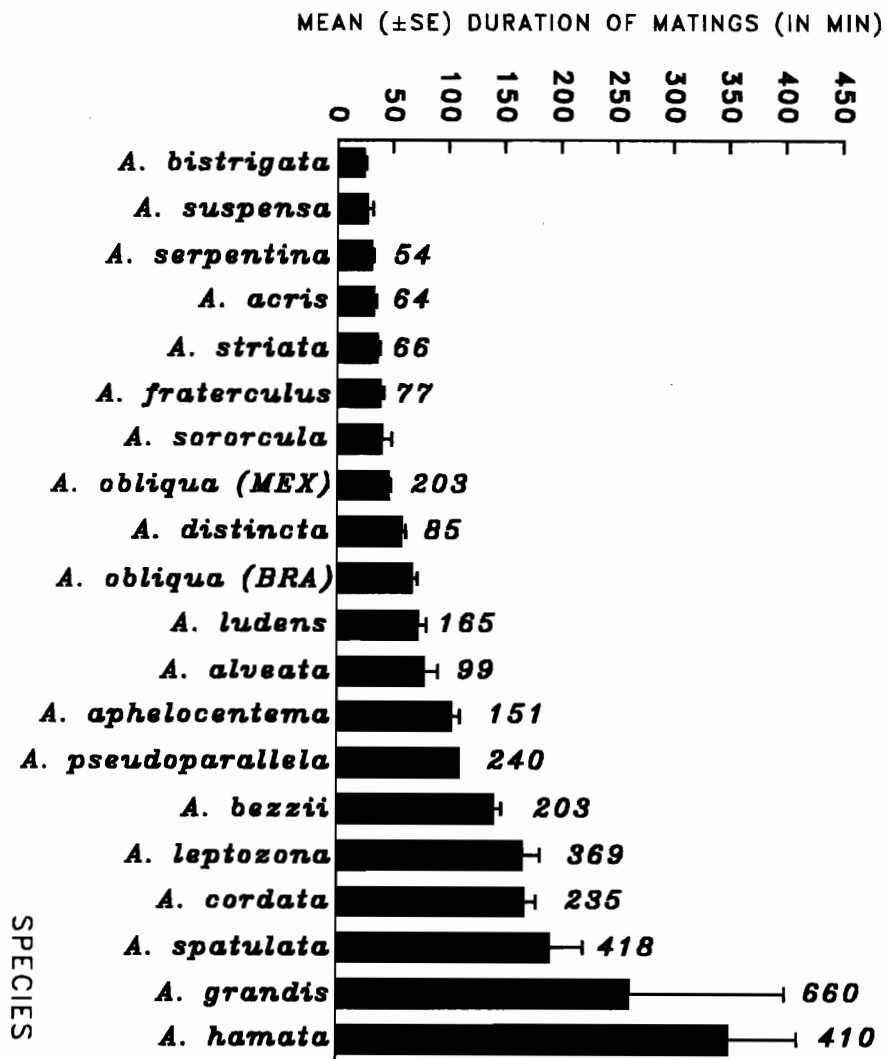


FIGURE 15.5 Copulation duration of 19 *Anastrepha* species. Information stems from the same sources cited in the Figure 15.2 caption.

sperm stores (Sivinski and Heath 1988). Recent work on *A. obliqua* and *A. ludens* revealed the female's refractory period to be regulated by mating status, size of male, feeding history of the male, fertility level of male (irradiated vs. unirradiated), and host availability (Robacker et al. 1985; Trujillo 1998). For example, 91% of the *A. ludens* females fed with protein and sugar mated at least once when in company of males fed with the same diet, whereas only 50% of the females mated when both sexes were fed on sucrose only. In the case of *A. obliqua*, 96% of females mated at least once, independently of the diet of either sex (Trujillo 1998).

15.8.15 ALTERNATIVE MATING STRATEGIES

Since in several species of *Anastrepha*, a minority of competitive/attractive males in leks obtain the majority of copulations, it may behoove the less competitive/attractive males to engage in alternative behaviors that give them a greater opportunity to mate (see Sivinski et al., Chapter 28). The examination of oviposition sites by male *A. suspensa* outside of the calling-lekking period

might be such an alternative means to locate females, although unsolicited sexual advances on fruits are rarely successful (Burk 1983; Hendrichs 1986). Robacker et al. (1991) failed to find any evidence of a similar alternative male strategy in *A. ludens*.

15.9 SHELTER SEEKING AND RESTING BEHAVIOR

Crawford (1918; 1927) already observed that flies always seek shelter during the heat of the day in the shaded sides of leaves (bottom surface), branches, and fruit. Flies seek out densely foliated trees and stay there until temperatures drop. At least with *A. striata* and *A. obliqua*, both sexes usually rest at the same time (Aluja et al. 1993; Aluja and Birke 1993). Resting occurs throughout the day (Malavasi et al. 1983; Aluja et al. 1993), and is influenced by the physiological state of the individual (e.g., after feeding it is common to see flies resting), its age, and environmental conditions. As noted before, recently emerged individuals tend to rest continuously for several hours while sexually mature ones do so intermittently throughout the day.

15.10 CONCLUSIONS AND FUTURE RESEARCH NEEDS

Perusal of the chapters on the behavior of various groups of tephritids reveals the remarkable parallels between *Anastrepha* and many other tephritids. If we borrow a concept from the taxonomists, it appears that there is a general behavioral ground plan in tephritids. Based on this ground plan, at least one species in every tephritid genus exhibits “variations on the general theme.” The same is even true when comparing behavior between two unrelated groups of flies: tephritids vs. drosophilids (Kaneshiro, Chapter 32). Here too, one is faced with the remarkable parallels in the behavioral repertoire between, for instance, some *Anastrepha* and *Drosophila* species. For example, when comparing the behavior of flies in the tephritid genera *Blepharoneura* and *Anastrepha*, we are struck by how similar certain body or wing movements are when encountering a conspecific or natural enemy or when alone. We specifically refer to holding raised wings in a stiff position (“arrowhead” posture), or to *hamation*, *enantion*, *supination* (synchronous and asynchronous), and *lofting* (*sensu* Headrick and Goeden 1994). For example, Condon and Norrbom (1994), reporting on the behavior of three sympatric species of *Blepharoneura*, show a picture in which a male of *B. atomaria* (Fabricius) pursues a female as she grazes on a leaf of a host plant. Remarkably, the position of the wings and body — stiff, raised wings and body in “attack position” (= “arrowhead” posture) — is almost identical to that observed in *A. striata* males when detecting a female in close proximity (see Figure 15.4; also see Aluja et al. 1993). To illustrate our point further, in *Anastrepha* there are species such as *A. fraterculus*, where males exhibit a neatly timed rhythm of *asynchronous supination* which is identical to the one exhibited by many flies in the subfamily Tephritinae (Headrick and Goeden 1994). For the evolutionary implications of the above, see Sivinski et al. (Chapter 28).

We would like to highlight the fact that our observations on the behavior of *Anastrepha* seem to mesh well with the phylogenies based on morphological characters and molecular data by Norrbom et al. (Chapter 12) and McPheron et al. (Chapter 13). For example, primitive *Anastrepha* species like *A. cordata* behave quite similarly to species in the probable sister group *Toxotrypana* (e.g., *T. curvicauda*). As discussed in this chapter and Chapter 12, it appears that the more primitive *Anastrepha* species attack latex-producing plants and feed preferentially on seeds. Seed feeding can be thus considered a primitive character. Interestingly, this character appears, on occasion, in derived species (e.g., *A. ludens* feeding on seeds of two of its native hosts). As more comparative information is accrued on the behavior of *Anastrepha*, it will be possible to map behavior onto the existing morphological and molecular phylogenies (Norrbom et al., Chapter 12; McPheron et al., Chapter 13). With this in mind, we recommend that any new study on the many species for which nothing is known consider a detailed quantification of the overall behavioral repertoire, and in

particular oviposition and mating behaviors. In the case of oviposition it would be particularly useful to describe and quantify drilling behavior, host-marking behavior or lack thereof, aculeus-cleaning behavior immediately before or after an oviposition bout, clutch size, and host-selection and acceptance behaviors. In the case of mating behavior, the following would be useful information: daily calling and mating rhythms, length of matings, body postures, wing movements (such as *hamation*), pre- and postcopulatory songs or lack thereof (when possible, making recordings for pulse-train analysis), existence of trophallaxis or lack thereof, and pheromone release and deposition behaviors and mechanisms. Of interest here, too, is the mating system (e.g., lek polygyny vs. resource-based polygyny). Aside from behavior, it would also be very useful to record systematically (i.e., using the same methodology) in each species certain basic traits such as sexual maturation periods, survivorship schedules, and gross and net fecundities.

As pointed out in the introduction, *Anastrepha* offers the unique opportunity to compare behaviors among many species. The wide gamut of calling/mating rhythms described here provides impressive evidence of this. It would be highly desirable for future studies to utilize a standard methodology to facilitate comparison and interpretation of behavioral patterns. For example, it would be important to select study species along phylogenetic lines, ideally picking primitive and derived species and always stressing the comparative approach. It is also highly desirable that a greater effort be made to study behavior under natural conditions. This entails several challenges. For example, in tropical evergreen forests, trees are very tall and costly observation towers would be required. But if we are truly to understand behavior in flies of the genus *Anastrepha*, we first need to observe their behavior in nature, thoroughly trying to identify the most important environmental factors that influence it.

A further step we need to take is to start dissecting the genetic basis of behavior. Intraspecific variability in mating success is large and it seems there are grounds to believe that there are alternative mating strategies, such as delaying the onset of calling or participation in leks (M. Aluja, unpublished data). Interspecific crosses could also prove rewarding when trying to identify ancestral behavioral characters. We also need to dissect behavioral rhythms in terms of their genetic vs. environmental components. For example, there are rhythms such as timing of ovipositional activities that seem to be quite plastic and strongly influenced by environmental factors such as temperature. In contrast, there are others, such as calling rhythms, that appear to be mostly driven by internal clocks. Finally, we need to start analyzing behavior in terms of energetics and to address the fascinating topic of cryptic female choice. In these areas, the work on *Ceratitis capitata* by B. Yuval and W. Eberhard and their collaborators has elegantly set the stage for future studies on *Anastrepha* (see Eberhard 1996; Yuval and Hendrichs, Chapter 17).

With respect to the wide gamut of *Anastrepha* calling rhythms mentioned above, there are several selective forces that could have played a role in shaping them. First, temporal isolation may play an important role in reproductive isolation between *Anastrepha* species, especially those occurring in sympatry (Selivon and Morgante 1997; Sivinski et al., Chapter 28). When males of a given *Anastrepha* species are placed in a cage with females of the "wrong" species, they readily attempt mating. Furthermore, at peak hours of mating activity, it is common to observe males attempting to mate with other males. It thus appears that there is no early discrimination by males of potential mating partners. Such discrimination occurs during close-range interactions between the sexes (for a thorough analysis of this see Eberhard, Chapter 18). We thus believe that temporal isolation is a very effective mechanism allowing *Anastrepha* species living in sympatry to reduce energy waste and costly errors in choosing the appropriate mating partner.

To document this, Sivinski et al. (Chapter 28) compared calling rhythms of some *Anastrepha* species living in sympatry and in allopatry. A good example of the first case is represented by *A. suspensa* and *A. obliqua*. The center of evolution for these highly derived species is arguably the Greater Antilles, where both can be currently found. Close analysis of their daily patterns of calling reveals an almost perfect reversed mirror image (see Figure 15.2). While *A. obliqua* calls

preferentially in the morning, *A. suspensa* does so in the afternoon hours. A similar pattern can be detected when comparing calling rhythms of *A. striata* and *A. fraterculus*, or by comparing those of *A. obliqua*, *A. ludens*, and *A. serpentina* (see Figure 15.2). In both cases, individuals of each species are likely to encounter each other because they either share a common host (*P. guajava* in the case of *A. striata* and *A. fraterculus*) or hosts, and resting or feeding sites (*M. indica* or mixed *M. zapota*, *Citrus* spp., and *M. indica* orchards in the case of *A. obliqua*, *A. ludens*, and *A. serpentina*). Note that the peak hour of calling never coincides. Another factor that could have played a role in shaping daily calling/mating rhythms is that many species never interact because of the fruiting phenology of their hosts. If such is the case, an overlap in calling rhythm would have no detrimental consequences.

Finally, a word on applied aspects of *Anastrepha* behavior. Based on the overwhelming behavioral diversity and complexity described in this chapter, it becomes clear that any attempt to mass rear *Anastrepha* needs to be coupled with highly sensitive quality control tests. These tests need to be oriented toward detecting consistency in a particular trait (e.g., mating success), as opposed to the narrow snapshots currently obtained with standard quality control tests. Our research clearly indicates that when studying a cohort of individuals over a period of time, what could be a competitive male on day 1 becomes uncompetitive 3 or 4 days later.

In conclusion, flies in the genus *Anastrepha* provide a unique, but to date not fully exploited, opportunity to study behavior using a comparative approach. First, there are potentially more than 200 species to be compared (Norrbon et al., Chapter 12). Second, the behavioral repertoire of those few species studied thus far is remarkably variable and complex. This could render the comparison of, for instance, mating or oviposition behaviors a highly rewarding endeavor. Comparing modalities of, for example, male calling or female aculeus dragging behavior between species could possibly allow the identification of apomorphic or plesiomorphic behaviors. Third, and as aptly discussed by Norrbom et al. (Chapter 12) and McPheron et al. (Chapter 13), the phylogeny of the group is now fairly well understood. This opens up the opportunity to compare formally behaviors between primitive and derived species and to attempt to construct a behavioral tree based on phylogeny. Fourth, and related to the latter, the behavior of *T. curvicauda*, a fly that belongs to the genus that may be the sister group of *Anastrepha* or may even fall within *Anastrepha*, is well studied. This allows interesting comparisons, and can provide clues to the possible evolutionary pathways of certain behaviors. Fifth, the genetics of behavior, a critical area when trying to unravel the evolution of behavior, can also be approached from a comparative perspective, since some species interbreed in the laboratory. This will allow us, at least in the near future, to determine the genetic mechanisms involved in controlling behavior. Sixth, both the sexual and host-marking pheromone systems of *Anastrepha* are currently being studied in depth (see Aluja et al. 1998; Heath et al., Chapter 29:). This will no doubt contribute to our knowledge on the phylogeny of the group, and will also allow us to understand how chemical barriers could have shaped interactions between species in nature.

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COLOR FIGURE 1



COLOR FIGURE 2



COLOR FIGURE 3



COLOR FIGURE 4



COLOR FIGURE 5



COLOR FIGURE 6



COLOR FIGURE 7A



COLOR FIGURE 7B



COLOR FIGURE 8



COLOR FIGURE 9

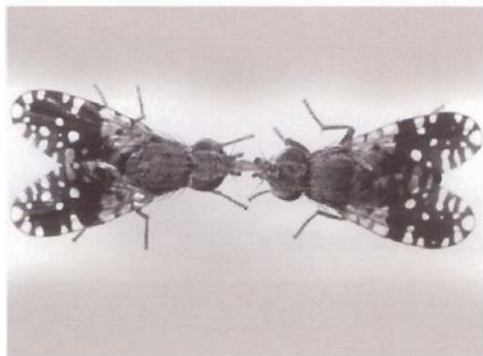


FIGURE 10



COLOR FIGURE 11



COLOR FIGURE 12



COLOR FIGURE 13



COLOR FIGURE 14A



COLOR FIGURE 14B



COLOR FIGURE 14C



COLOR FIGURE 15A



COLOR FIGURE 15B



COLOR FIGURE 15C



COLOR FIGURE 15D



FIGURE 16



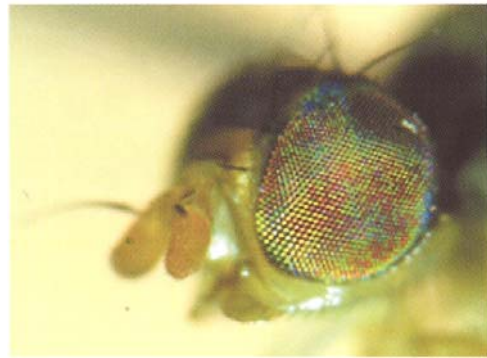
COLOR FIGURE 17



COLOR FIGURE 18



COLOR FIGURE 19



COLOR FIGURE 20



COLOR FIGURE 21A



COLOR FIGURE 21B



COLOR FIGURE 21C



COLOR FIGURE 21D